The vegetation of Connecticut.
VII. The associations of depositing areas along the seacoast *

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(WITH TEN TEXT FIGURES)

CONTENTS

I. INTRODUCTION

In a previous paper of this series† the writer has discussed the plant associations of eroding areas along the Connecticut coast, and the present paper is practically a continuation of that one. As pointed out there, the lateral distribution of the various types of seaside plant association is determined mainly by differences in physiography, their vertical distribution mainly by differences in tide level. For purposes of treatment these associations are grouped primarily with reference to their physiographic relations, secondarily with reference to their relation to tide levels. A general discussion of the ecological relations of seaside plants and associations is included in the previous paper, which also contains a list of the literature cited in the present article.

The physical character of the shore and bottom in depositing

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areas varies with the degree of exposure and the nature of the tidal currents. In the more sheltered situations, as in embayments and behind barrier beaches, the deposit is mostly muddy; in less sheltered situations, as along parts of the shore which face on the open Sound, it is mostly sandy; in relatively exposed situations it may be stony. Broadly speaking, all portions of a depositing oceanic shore, which lie above low tide level and below the topographic form produced by agencies other than the sea, may be classed as beach.* Popularly, however, the term beach is generally applied only to sandy or stony shores, and in this sense it will be mainly used in the present paper, muddy shores (in so far as they are associated with the tidal marshes) not being classed as beach. As above defined, the beach includes only areas of water-deposited material; but the concept may conveniently be extended to embrace the contiguous areas of wind-blown sand which commonly overlie the higher portions of the beach proper. Beaches may take the form of spits and off-shore barriers, or they may fringe the mainland. In the latter case, the upper limit of the beach proper is usually marked by a line of bluffs or sand dunes.

II. THE VEGETATION OF DEPOSITING AREAS AND ITS ECOLOGICAL RELATIONS

A. STONY BOTTOMS AND BEACHES

1. Associations of the sublittoral region

There are occasional areas of stony bottom which seem to have originated through a process of aggradation rather than one of degradation, but it is well nigh impossible to draw sharp lines of demarcation between the two types. On the whole, stony bottoms are much more characteristically associated with eroding portions of the coast than with portions in which deposition predominates: in either case they are developed only in fairly exposed situations, and in both cases the character of the vegetation is essentially the same (see preceding paper of this series, p. 109).

* In this connection, see especially discussion of Lake Michigan beaches by Cowles ('99, pp. 112 et seq.), of Long Island beaches by Transeau ('13), and of sand formations on marine coasts by Olsson-Seffer ('10a). Cowles, defining the beach in the sense given above, distinguishes between xerophytic and hydrophytic beaches. Transeau defines the beach as including "all of the areas occupied by the shore drift in transit."

2. Associations of the littoral and supralittoral regions

The associations of shingle beaches.—Along coasts which are open to the ocean, beaches of this description—built up very largely of water-rounded stones, ranging in size from pebbles up to cobbles six inches or more in diameter, that have been cast ashore by the heavy seas of winter storms—are the common type.* Even along the relatively sheltered Connecticut coast the beaches of comparatively exposed situations commonly are more or less gravelly or stony,† but typical shingle beaches are infrequent. The best example known to the writer is at Compo Beach, Westport—a rather surprising location, since it lies well toward the head of the Sound. Here there has been built up a stony spit, perhaps a hundred yards wide and rising five or six feet above ordinary high tide level, which extends out from the mainland about a quarter of a mile in a direction approximately at right angles to the southeasterly winds which here sweep unobstructed across the Sound. The windward slope of this spit is typical shingle, consisting, in the supralittoral, of pebbles and small cobbles.‡ Its vegetation is sparsely developed, comprising a small number of herbaceous xerophytes which grow scattered over the portion of the beach above high tide level. The following species are characteristic:

Chenopodium album	*Lathyrus maritimus*
Atriplex patula hastata	*Solidago sempervirens*
Salsola Kali	*Ambrosia artemisiifolia*
Cakile edentula	*Xanthium canadense*

On the lee slopes of the spit the substratum is a mixture of stones, gravel, and sand, and here the vegetation, while very open, is somewhat more luxuriant, including in particular a varied assort-

* Shingle beaches are well developed, for example, along the Cape Breton coast, where they have been described in some detail, with several figures, by the writer ('18, pp. 324–330).

† But the stony "beaches" which commonly are developed along the base of eroding bluffs of glacial drift are built up, not of materials washed ashore by the waves, but of boulders and stones, originally a part of the heterogeneous mass of rock waste which comprises the drift, that have been left behind when the finer materials were washed out and carried away by the waves. The gradual accumulation in this way of boulders along the base of an exposed bluff may come to form an effective protection against excessive wave action.

‡ It has not been possible to visit this beach at low tide, so that the littoral region has not been studied. Presumably its vegetation is similar to that of stony shores in the littoral as elsewhere described (Nichols, *l.c.*, p. 111).

ment of weeds. The following plants were noted as frequent or common, of the weeds only the more important being listed:

Juniperus virginiana	*Trichostema dichotomum*
Poa compressa	*Linaria vulgaris*
Carex silicea	*Erigeron canadensis*
Polygonum aviculare	*Gnaphalium polycephalum*
Polygonella articulata	*Ambrosia artemisiifolia*
Trifolium arvense	*Achillea Millefolium*
Lathyrus maritimus	*Artemisia caudata*
Oenothera sp.	*Taraxacum officinale*

Among other plants which ordinarily occur in similar situations elsewhere are the bayberry (*Myrica carolinensis*), the wild rose (*Rosa virginiana*), the cherry (*Prunus serotina*), various species of *Rhus*, and the mullein (*Verbascum Thapsus*).

B. SANDY BOTTOMS, BEACHES, AND DUNES

1. Associations of the sublittoral region

Sandy bottoms may be quite barren of vegetation, or they may support a usually scattered growth of eel grass (*Zostera marina*). This plant grows most luxuriantly on the muddy bottoms of sheltered waters, and its ecological relations will be discussed in connection with these; but it is apt to occur, locally at any rate, even in exposed situations, wherever there are deposits of sand or mud in which it can find foothold for its roots. Sand does not afford a favorable substratum for seaweeds; but as a rule these are represented by various of the species elsewhere noted as characteristic of eroding rocky or stony bottoms, here growing attached to shells or scattered stones, and also by forms which are epiphytic on the eel grass (see p. 523).

2. Associations of the littoral and supralittoral regions

Introductory.—Three subdivisions of the beach are commonly distinguished: the lower, the middle, and the upper beach. Along the seacoast, on sandy (or stony) depositing shores, the lower beach coincides approximately (but not exactly) with the littoral region, the middle beach with the lower supralittoral, the upper beach with the upper supralittoral.* These subdivisions are well brought out in FIG. 1.

* Olsson-Seffer ('10a) designates "that portion of the beach that lies below mean low tide, but which may be exposed by neap [*sic*] tides" as the "submerged beach," and terms the lower beach the "front beach."

n on the lower beach.—Edaphic conditions
ment of vegetation of any description on
a sandy shore. Halophytic seed plants,
ne littoral region along muddy shores, are
foothold in the shifting sand, constantly
the waves, and the algae likewise find
. With local exceptions, the lower beach
visible plant life.

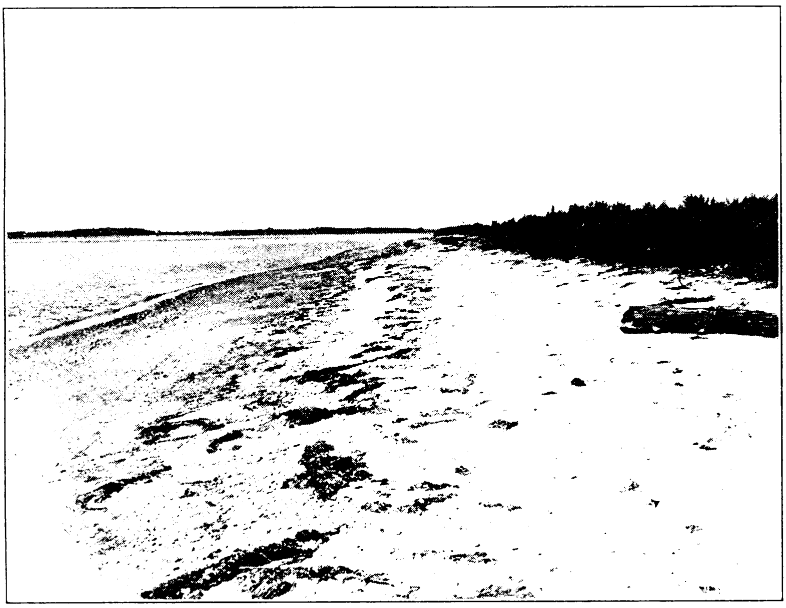

FIG. 1. Sandy beach along relatively exposed seaward side of spit at Old Lyme; low tide. Upper limit of lower beach marked by line of tidal trash; middle beach here supporting very scanty plant population; dune beach (above) covered with *Ammophila*, etc.

Associations of the middle beach.—The lower beach is usually described as extending upward as far as the highest point reached by the waves of summer storms, and the middle beach as reaching from here to the upper limit of the winter storm waves. The actual position of these boundaries, of course, changes more or less from year to year. Because of the usual abundance of driftwood and other riff-raff, the middle beach is termed the "drift beach" by Jennings ('09). During summer this area

is undisturbed by wave action, but during winter it is frequently swept by the sea and sometimes becomes completely covered over with ice. Obviously conditions here are not suitable either for seaweeds or for perennial land plants. The characteristic inhabitants are xerophytic annual seed plants: species which in divers ways* are adapted to withstand the exposure to strong winds, intense illumination, and high temperatures to which plants growing on the open beach are constantly being subjected during the growing season.† The plant cover on the middle beach is

* Adaptation to a xerophytic environment on the part of beach and dune plants is seen particularly in their peculiarities of leaf structure. Thus, of the various species to be listed as characteristic of middle or upper beach, *Salsola*, *Cakile*, and *Arenaria* have leaves which are conspicuously succulent, *Atriplex* and *Lathyrus* have semi-succulent leaves, and *Xanthium* has hard, thick leaves; the leaf surface in *Chenopodium* and *Atriplex* is covered with a granular-waxy coating, and in *Euphorbia* and *Lathyrus* with a waxy "bloom;" the leaves of *Artemisia Stelleriana* are densely tomentose; while those of *Ammophila* are erect, stiff, and conspicuously involute. Moreover, in *Euphorbia* the entire aërial system of the plant exhibits a prostrate "radiant" habit—a habit also possessed, though to a less pronounced degree, by the shoot in several other beach plants. In addition to these peculiarities of the shoot system, which are associated either with the storage of water or its conservation (through reduction of transpiration), the root system in beach and dune plants is so developed as to make the most of the available water supply: a supply which, though scanty in the surface layers of sand, is usually quite abundant at depths of from six inches to a foot. The various annual species have a prominent tap-root, as have some of the perennials, and the usually abundant secondary roots radiate horizontally for considerable distances. Paucity of mineral and organic nutrients in the soil doubtless is a factor which markedly affects the character of beach and dune vegetation, and which may be largely responsible for the absence here of many plants that are found in dry soils elsewhere.

† For many years the plants of sea beaches, like those of salt marshes, were generally regarded as true halophytes. Kearney ('04), however, has shown that the amount of salt present in the sand of the middle and upper beaches at the height of the growing season is in reality very slight. At a station along the Massachusetts coast, in July, for example, the sand of the middle beach, near the lower limits of vegetation, was found to contain only 0.003 per cent, or less, of salt (as compared with 1.4–2.6 per cent in the soil of a nearby salt marsh). At certain seasons, of course, salt may be present in relatively large amount, but in regions of abundant precipitation it is rapidly leached out by percolating rain water. The plants of sea beaches, then, "are not generally halophytes, in the same sense that the plants of inland saline situations are, but are for the most part merely such plants of normally non-saline habitats as are able to withstand a high salt concentration without injury" (Bartlett, '09). Nevertheless, it is a fact, to quote further from Bartlett, "that a large proportion of the species of the beach and transition zone floras, although not necessarily always found within the limits of tide water, are, nevertheless, seldom found more than a few miles from the ocean." Bartlett suggests that it may be

best developed toward its upper margin, but even here, as a rule, the sand is only sparsely populated. Common species are the following:

Chenopodium album		*Salsola Kali*	*f*
" *leptophyllum*	*f*	*Cakile edentula*	*f*
Atriplex arenaria		*Euphorbia polygonifolia*	*f*
" *patula hastata*	*f*	*Xanthium canadense*	*f*
" " *littoralis*	*f*		

Associations of the upper beach.—The upper beach (FIGS. 1, 2) lies beyond reach of the waves at all seasons. Chronologically, it is the oldest part of the beach: it has been built up by wave-washed sands in former years, but is now protected by the middle and lower beaches.† As a habitat for plants the upper beach differs from the middle beach chiefly in its freedom from the mechanical effects of wave action, by reason of which it is possible for perennial species to exist here. The distinctive plants, frequently found also on the shoreward reaches of the middle beach, are four xerophytic perennial herbs: the sand reed or beach grass (*Ammophila arenaria*), the beach pea (*Lathyrus maritimus*), and, east of New Haven, the sandwort (*Arenaria peploides*) and the dusty miller (*Artemisia Stelleriana*). These, with various members of the middle beach flora, usually form a sparse, open covering over the sand.

Associations of the dune beach.—Along most sandy shores the upper beach, as a distinct topographic form, is practically absent,

necessary to alter somewhat our conception of what constitutes a halophyte, and that, while it may be impossible to correlate geographic ranges of beach plants with their adaptability to grow in highly saline situations, the possibility of some such correlation becomes greater if the ratio of saline constituents in the soil water, irrespective of their absolute concentration, be taken as a criterion, rather than absolute salinity. Thus a very slight admixture of sea water with an average soil water (in which the concentration of mineral salts is very slight) would be sufficient "to bring the ratio of elements into approximate agreement with sea water" (for further discussion, see Bartlett, *l. c.*, p. 223).

It is worthy of remark, in this connection, that a very considerable number of the plants which characterize the beaches and dunes along the New England coast are characteristic of similar situations along the Great Lakes, where soil salinity as an environmental factor is out of the question.

* Species marked "*f*" are characteristic of beaches along the Great Lakes.

† As with other portions of the beach, the lower boundary of the upper beach is subject to change, since in times of exceptionally severe storms the sea may sweep over areas which hitherto have been undisturbed by wave action for long periods.

since, almost invariably, all portions of the beach beyond reach of the waves quickly become covered over by aeolian deposits: by wind-blown sands which the on-shore gales catch up from the middle beach and sweep landward. In this way there originates what may appropriately be designated the *dune beach*: an area distinguished primarily by the presence of sand dunes.*

FIG. 2. Somewhat muddy beach along relatively sheltered landward side of spit shown in FIG. 1; tide not quite low. *Spartina glabra* forming an incipient marsh in midlittoral; *Ammophila* on dune beach above; intermediate beach nearly barren of vegetation.

Probably the finest dune beaches in the United States are those of the Lake Michigan region, the physiographic and ecological relations of which have been so admirably portrayed by Cowles ('99). There the dune areas constitute an important geographic feature, extending for long distances along the southern and eastern shores of the lake and in places reaching inland for more than a mile. These dunes frequently attain elevations of a hundred

* The term dune beach has been used by Ganong ('06) in a somewhat more restricted sense than that in which it is used by the writer.

and sometimes as much as three hundred feet. Similar dune complexes have been developed along various exposed shores on the Atlantic coast, as at Ipswich (see Townsend, '13) and Cape Henry (see Kearney, '01), but nothing comparable is to be met with along the relatively sheltered Connecticut coast. Here the dune beach ordinarily is little more than a broad, rounded, more or less continuous ridge of sand, from fifty to 250 feet wide, lying between the middle beach and the contiguous ordinary uplands, or, when developed on barrier beaches or spits (FIG. 2), separated from the mainland proper by lagoons or salt marshes. These low, ridge-like dunes seldom rise more than six feet above high tide level.* Their outer face usually is steep and irregular, due to the constant tendency which they exhibit to advance seaward, into the area occupied by the middle beach, where they become exposed, at periodically recurring intervals, to the battering of storm waves. The steep lee slopes characteristic of so many dunes are scarcely apparent in these low Connecticut dunes. Only occasionally is there developed more than a single dune, or line of dunes, and then the inner, shoreward dunes are scarcely worthy of the name.

But in spite of their geographic insignificance the dune beaches of the Connecticut coast are not without interest, and their vegetation has many points in common with that of more pretentious dune areas in other regions. As elsewhere along the northern Atlantic coast, the distinctive plant of the dune beach is the sand reed, which commonly predominates the landscape in all directions. But, although invariably foremost in abundance, and the species which primarily determines the aspect of the vegetation, this coarse grass never grows in sufficient density to crowd out other plants. Viewed at close range, its erect clumps of foliage are seen to be separated from one another by patches of bare sand, thus affording ample space for various other herbaceous species to develop, and these are present in locally varying abundance. Especially prominent in their effect on the general

* Larger and much more typical dunes are developed near Watch Hill, Rhode Island, but a few miles from the eastern boundary of Connecticut (see *f. 1* in the preceding paper of this series). Some of these Rhode Island dunes are forty feet or more in height.

aspect of the vegetation are the beach pea, the evening primroses (*Oenothera muricata* and *O. Oakesiana*), the blazing star (*Liatris scariosa*), the seaside golden rod (*Solidago sempervirens*) and the wormwood (*Artemisia caudata*), to which may be added, among others, the following:*

Panicum amaroides	*Cakile edentula*
Triplasis purpurea	*Strophostyles helvola*
Eragrostis pectinacea	*Lechea maritima*
Cyperus filiculmis macilentus	*Teucrium canadense littorale*
" *Grayii*	*Verbascum Thapsus*
Carex silicea	*Erigeron canadensis*
Polygonella articulata	*Gnaphalium polycephalum*

As an environment for plants, the dune beach, during the growing season, is almost as unfavorable a habitat as the middle and upper beaches, and its vegetation is predominantly xerophytic. While the sand reed, with its herbaceous associates, usually predominates on the higher, more exposed sites, shrubs commonly occupy a prominent place in the more sheltered situations, as in the lee of the dune ridge, frequently forming dense thickets to the exclusion of much of the herbaceous vegetation. Particularly is this true of the beach plum (*Prunus maritima*), which usually is the most characteristic woody plant of the dune beach. The bayberry and the poison ivy (*Rhus Toxicodendron*) likewise grow in local profusion here, while the wild rose (*Rosa virginiana*) and sumacs (*Rhus* spp.) may be well represented. The false heather (*Hudsonia tomentosa*), a distinctive dwarf shrub of dune beaches in Rhode Island and elsewhere, is a comparative rarity along the Connecticut coast. Bryophytes and lichens are but sparingly represented by such species as *Ceratodon purpureus* and *Cladonia sylvatica*.

3. Successional relations along depositing sandy shores

The relatively rapid physiographic changes that ensue in the course of time along a depositing sandy shore, and the changes in the nature of the plant habitats which result, are accompanied by corresponding changes in the character of the vegetation, which

* From this list have been omitted various naturalized weeds which are characteristic of beaches, and also a number of comparatively rare native plants that belong here.

progressively increases in permanence and complexity. As the lower beach becomes built outward and upward, the gradually rising surface of sand becomes colonized first by the annual plants of the middle beach, which later are joined by the herbaceous perennials of the upper beach. With the development of the dune beach the plant population is still further augmented, and, under favorable conditions, shrubs may supplant herbs as the predominant growth forms. Only occasionally, in Connecticut, however, are trees met with on the dune beach, and forests never. In the development of the dune beach the vegetation itself plays an important rôle. The birth of a dune may be caused by the presence on the upper beach of any obstruction, such as a piece of driftwood, which interferes with the sand-laden winds sweeping landward, causing them to drop part of their burden. Thus, it commonly happens that the coarse, stiff, upright clumps of the sand reed, growing in local profusion on the upper beach and acting in the nature of a wind-break, bring about a local accumulation of sand and thereby inaugurate the development of a dune. But not only this. As the sandy surface is built upward, the grass, spreading by means of subterranean rhizomes, keeps pace with it, contributing further to the permanceny of the dune by the action of its copious slender roots, which bind the loose sand together, thereby fixing it in place.

C. MUDDY BOTTOMS AND SHORES, AND COASTAL SWAMPS

Introductory.—Among the outstanding physiographic features of the Connecticut coast is the extensive development of coastal swamps, typically represented by the salt marshes (FIGS. 4, 5, 6, 9). "Because of their lack of relief and uniformity of appearance", swamps of this description, in the words of C. A. Davis ('10), may appear "monotonous and uninteresting in the extreme"; yet it is only to the most superficial observer that they are entirely devoid of interest. Even as scenic features the monotony of the salt marshes is almost wholly one of topography, while from a scientific point of view these swamps, with their associated muddy flats and bottoms, present a diversity of fascinating problems, both biological and geological. According to figures given by Shaler ('85) there are fully 20,000 acres of coastal swamp in Connecticut.

In the account which follows, dealing primarily with the coastal swamps along the Connecticut shore, only those swamps are included whose vegetation is influenced, in some way or other, by the tides, or which are more or less intimately related to swamps of this type. As thus defined, coastal swamps along oceanic shores can be differentiated into three intergrading classes: *salt water swamps*, *brackish water swamps*, and *fresh water swamps*.* Salt water swamps are those whose surface is overflowed at more or less regular intervals (typically, twice each day) by practically undiluted sea water. Brackish water swamps are developed in situations where the inflowing tidal waters from the sea meet and intermingle with the outflowing fresh waters of inland streams or springs. Fresh water coastal swamps are developed either in situations where the ground is saturated with fresh water, derived from underground springs, and where the surface is overflowed so infrequently, or by saline water so dilute, that the freshness of the water in the soil is not affected; or else along the lower courses of rivers, in places where the influence of the tides in backing up the river water leads to the periodic inundation of the ground by fresh water.† The vegetation of salt and brackish water swamps in temperate regions is almost wholly herbaceous, consisting predominately of various grasses and grass-like plants. For this reason they are generally referred to as *marshes*. Popularly, both salt and brackish marshes are indiscriminately termed salt marshes. The vegetation of fresh water coastal swamps, in their most typical development, is likewise marshy; but some wooded swamps are also included in this group.

1. Associations of the salt marsh series

The muddy bottoms of the sublittoral.—The most distinctive plant of muddy bottoms along the seacoast is the eel grass (FIG. 3). As already noted, this also grows on sandy bottoms but it never attains there the luxuriance which it exhibits where growing on muddy bottoms. From mean low tide level, or slightly above,

* Shaler ('85, p. 361) distinguishes three classes of coastal swamps: salt water swamps, fresh water swamps, and estuarine swamps. From an ecological standpoint this grouping does not appear to the author as logical as the one here proposed.

† Swamps of the latter type are estuarine swamps, but so also may be the brackish swamps developed in similar situations further downstream.

the eel grass ranges downward to considerable depths, being recorded by B. M. Davis ('13) as growing in water as much as 75 feet deep in the Woods Hole region; but it is in the upper sublittoral that it flourishes best. So prolifically does it thrive in the shallow waters of protected harbors and coves that at low tide large areas of muddy bottom here will be almost completely hidden by its clusters of long, slender leaves. The eel grass is important on muddy bottoms, not merely because it is the dominant member

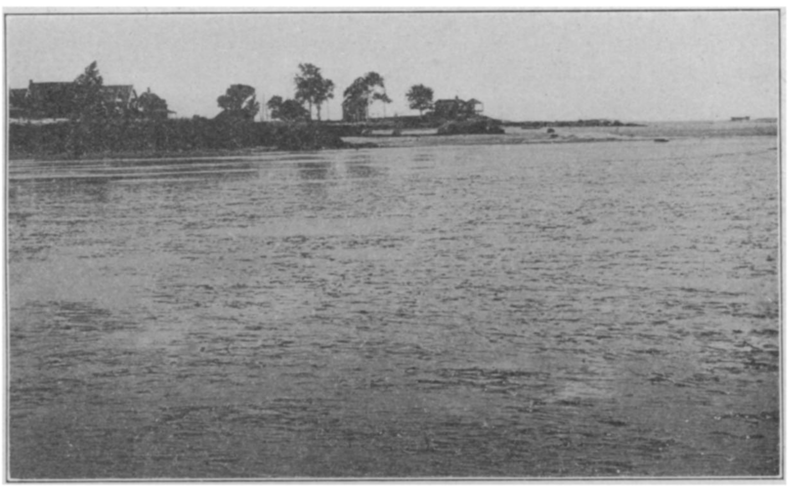

FIG. 3. *Zostera marina* on depositing bottom; leaves floating on surface at low tide. Orange.

of the flora, but also because it furnishes a substratum upon which many seaweeds, which otherwise would be absent, are able to grow. In the preceding paper of this series (*l.c.*, lists on pp. 102, 104), attention has been called to the fact that many of the algae of rocky bottoms grow also as epiphytes on the eel grass. These latter occur in association with the eel grass on muddy bottoms, some of them being more abundant here, at certain seasons, than on rocky bottoms. In addition to these, there are a number of the brown and red algae which grow exclusively as epiphytes on the eel grass, or more abundantly here than on any other type of substratum. Such are the following:

BROWN ALGAE (*Phaeophyceae*)

Punctaria latifolia

RED ALGAE (*Rhodophyceae*)

Chantransia virgatula	*Polysiphonia Harveyi*
Callithamnion byssoideum	" *Olneyi*
" *corymbosum*	*Melobesia Lejolisii*
Ceramium fastigiatum	

But while algae may grow in great profusion on the leaves and stems of the eel grass, in the shallow waters of the upper sublittoral these attached forms may be overshadowed, both in mass effect and in ecological importance, by certain species which grow entirely unattached, notably by the enteromorphas and the sea lettuce (*Ulva Lactuca*). *Enteromorpha clathrata* in particular commonly grows as an epiphyte on *Zostera*, but these attached plants are usually small. Like *Ulva*, which germinates on rocks, piles and the like, just as soon as an attached enteromorpha plant reaches any size it is usually torn away from its support by currents or waves and thereafter is at their mercy. These free-floating plants commonly settle in large numbers in quiet shallow waters where they apparently find conditions exceedingly congenial to their further growth. The sea lettuce forms crumply sheets, commonly more than a foot and sometimes, according to Johnson and York ('15), as much as thirty feet in diameter. The enteromorpha similarly forms dense tangles which, with the sea lettuce, may cover large areas of bottom, sometimes to the exclusion of the eel grass. The ecological relations of the eel grass, sea lettuce and enteromorphas are discussed in detail by Johnson and York ('15, pp. 18 et seq.).

The tidal flats of the lower littoral.—In their treatment of the marine vegetation at Cold Spring Harbor, Johnson and York ('15) divide the littoral region into three sub-regions: the *lower littoral*, the *midlittoral* and the *upper littoral*. In the present account, thus far, little attempt has been made to differentiate between lower littoral and midlittoral, the former term having been used to cover both these divisions. But along muddy shores sharply defined differences in the character of the vegetation make such a distinction imperative. The lower littoral here may be defined as the region extending from approximately mean low tide mark upward nearly to half tide level: it embraces the stretch of "mud flats" which intervenes between the muddy bottoms

below, on which the aquatic eel grass is the character plant, and the salt marshes above, in which terrestrial grasses are the predominant forms. At ordinary low tides these tidal flats of the lower littoral present a surface of soft, blue-black, ill-smelling mud—an area in which, except for local colonies of eel grass or salt marsh grass (*Spartina glabra*), seed plants and attached algae are practically absent. At certain seasons these muddy flats may be destitute of visible vegetation of any description; but at others the bare mud at low tide is littered with loose sheets of *Ulva* and tangles of *Enteromorpha*, which may cover the ground so thickly that, when viewed from a distance, the surface appears verdant green. The failure of the eel grass to flourish on tidal flats is probably associated with its inability to withstand the desiccation and extreme temperatures to which plants growing here are frequently subjected at low tide. The influence of these factors must also react unfavorably on *Ulva* and *Enteromorpha*, but the loose carpet of vegetation which these form is constantly being renewed by fresh plants washed in by the tides and currents. The inability of the salt marsh grass, character plant of the next higher zone, to colonize the flats, is probably due to the inadequate aeration, particularly of its subterranean organs, at these lower levels (see detailed discussion in Johnson and York, '15).

The midlittoral marsh.—Salt marshes are typically developed on muddy bottoms, between approximately mean half and high tide levels, and their vegetation, taken in its entirety, is characterized by the predominance of perennial grasses or grass-like plants. The nature of the plant cover exhibits certain striking differences, however, primarily in relation to tide levels (FIG. 4). At the lower levels, in the region of greatest tidal play, the vegetation is made up largely of coarse, reedy grasses, between three and five feet tall; at the higher levels it consists mainly of finer, lower grasses and grass-like plants, mostly under a foot in height. The area occupied by the reedy grasses, extending from the lower limits of the marsh upward to within a few inches of the level reached by ordinary high tides (approximately to neap high tide level), may be designated the *midlittoral* or *reed marsh*; while the area occupied by the finer grasses, comprising the higher surface of the marsh, may be termed the *upper littoral marsh* or *meadow*.

In passing upward from tidal flats to midlittoral marsh there is a marked change, not only in the nature of the vegetation but in that of the substratum. The soft, structureless ooze of the lower levels gives way to a peaty or semi-peaty soil, muddy but relatively firm, composed partly of silt and partly of plant remains,

FIG. 4. Tidal creek, with border of *Spartina glabra*, and salt meadows. East Haven. View taken at low tide.

the whole being more or less compactly bound together by the thick underground stems of the reed-like grasses with their copious, long, slender roots. This transition ordinarily is quite abrupt. Commonly there is a low but distinct terrace-like effect where the midlittoral marsh impinges on the tidal flat, while along tidal creeks in particular the surface of the midlittoral marsh usually slopes sharply upward from the flats, forming steep banks frequently a couple of feet high. These steep banks are a direct result of the observed differences in substratum in relation to various agencies of erosion; for even along a shore where deposition predominates there is usually more or less local or periodic erosion associated with the shifting of tidal currents, the ebb and flow of

the water through tidal creeks, and the action of ice. The soft, unconsolidated mud of the flats offers little resistance to erosion, while the relatively firm, compacted soil of the midlittoral marsh withstands it to a considerable degree. It is only in situations where erosion phenomena are virtually negligible at all seasons that the transition between tidal flats and midlittoral marsh is gradual.

FIG. 5. *Spartina glabra* midlittoral marsh in New Haven harbor. View taken at high tide.

The character plant of the midlittoral marsh is the salt marsh grass (*Spartina glabra* vars. *pilosa* and *alterniflora*). This coarse grass everywhere forms a rank, fringing growth along the outer borders of the marsh and along the tidal creeks (FIG. 4). Ordinarily it occupies a narrow strip, a few yards wide at the most, but frequently, on gently sloping ground, it covers large areas (FIG. 5). Other seed plants are conspicuously absent from the midlittoral marsh, but the salt marsh grass seems peculiarly adapted to this habitat, where the ground is inundated, on an average, from five to sixteen hours daily and where, at the lower levels, the entire plant may become submerged at high tide. Toward the upper border of the midlittoral zone, however, the algae

may comprise an important element in the flora. *Vaucheria Thuretii* and *Rhizoclonium* spp. frequently form felt-like growths over the soft muddy substratum, or else, with other species, such as *Cladophora expansa* and *Enteromorpha clathrata*, build loose, tangled mats of vegetation. As at lower levels, loose plants of *Enteromorpha* and *Ulva*, drifting in with the currents and settling down amid the *Spartina* stalks, may maintain a more or less evanescent existence. The rockweeds (*Fucus* and *Ascophyllum*) may also be well represented in the upper reaches of the midlittoral marsh, either by loose specimens or by plants that have become partially buried in the mud and thereby fixed in place.*

The upper littoral marsh.—When viewed from a distance, the meadowy surface of the upper littoral marsh (FIGS. 4, 6, 9) appears to be flat, except where it is interrupted by the tidal creeks, which commonly meander through it, or by tidal pools and artificial drainage ditches. But the ground is not absolutely flat; invariably it is gently undulating. For the most part the differences in surface elevation are very slight (but an inch or a few inches at most), yet they are sufficient to have an important effect on the drainage and wetness of the marsh surface, on the aeration and salinity of the substratum, and thereby on the nature of the ground as an environment for plants.† The substratum here is firm and peaty, being made up largely of compactly interwoven rhizome and root remains.

* The rockweed flora of salt marshes is of peculiar interest and has been the occasion of considerable study. Not only may these seaweeds, ordinarily associated with rock shores, form an essential part of the midlittoral salt marsh vegetation, but they develop here certain remarkable features which are not found elsewhere. In general these marsh-dwelling fucoids are characterized by their pronounced tendency to reproduce vegetatively, the absence of sexual reproduction, their dwarf habit, the lack of an attachment disc, and spirality or curling of the thallus. For detailed discussion and references to the literature, see Baker and Blandford ('16).

† The distribution of salt and brackish marsh plants is conditioned even more by the salinity of the soil water than by that of the water which floods the surface of the marsh. The salinity of the soil water is affected not only by the concentration of the water which overflows the surface of the marsh but by the length of time the surface is uncovered, the drainage relations, and by the presence or absence of subterranean supplies of fresh water. In a salt marsh at Cold Spring Harbor, Transeau ('13) found the salt content of the soil water in the *Spartina patens* association to be but 75 per cent as great as that of the harbor water, and in the *Juncus Gerardi* association but 57 per cent. See further observations by Bartlett ('09), Johnson and York ('15), Nichols ('18), and especially by Harshberger ('11).

Except locally, as along tidal creeks and ditches and in poorly drained depressions, the salt marsh grass is not present in salt meadows, where the ground ordinarily is flooded with saline water from but one to four hours daily, and then to a depth of only a few inches. Just what factors limit the upward distribution of this plant are uncertain. It may be the lessening salinity of the soil water (but, in this connection see remarks on p. 535); it may be the relative dryness of the soil at higher levels; it may

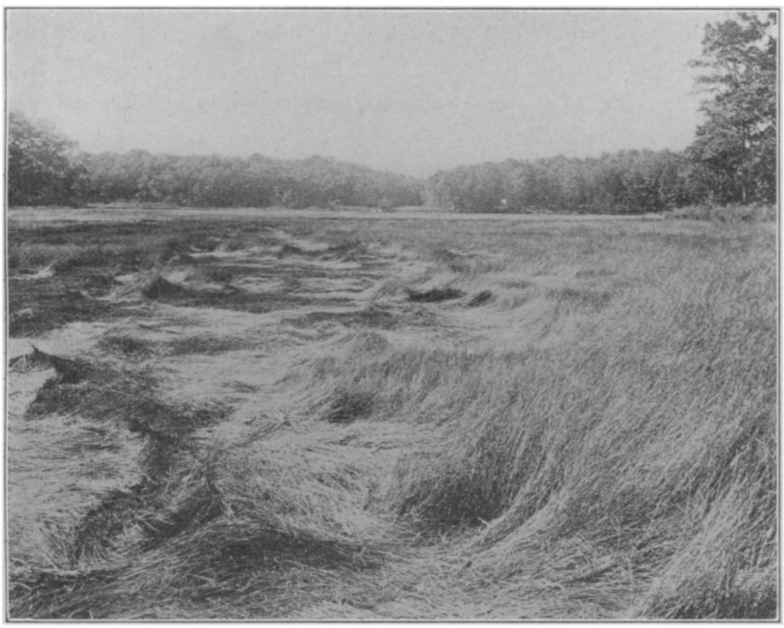

FIG. 6. Salt meadows, showing the billowy effect produced on the vegetation by winds and tidal currents. East Haven. *Juncus Gerardi* (right), *Spartina patens* (left).

be its inability to compete successfully with the salt meadow grasses; it may be a combination of factors (see Johnson and York, '15, pp. 48 et seq.) The predominant plants of the upper littoral marsh are three: the salt meadow grass (*Spartina patens juncea*), the alkali grass (*Distichlis spicata*), and the so-called black grass (*Juncus Gerardi*). These typically form a luxuriant meadow-like sward (FIG. 6). But while the three sometimes grow intermixed, they differ from one another in their ecological requirements

and, as a rule, one or another predominates locally. The salt meadow grass commonly comprises the bulk of the meadow vegetation, being especially characteristic of areas which are submerged several inches at ordinary high tides but where the water drains away rapidly between tides. The alkali grass is particularly characteristic of situations which likewise are submerged several inches at ordinary high tides, but where the water drains away more slowly than from the areas occupied by the salt meadow grass. The black grass thrives on the higher parts of the meadows, especially in areas which are barely reached by ordinary tides. It commonly forms a definite zone of vegetation along the landward borders of the meadow (see p. 533), though by no means restricted to this region.

Any one of the three species just mentioned may occupy considerable areas to the practical exclusion of everything else; but as a rule the grassy sward is dotted here and there with other seed plants which, if less abundant, are quite as distinctive. Particularly characteristic of salt meadows along the Connecticut coast are the following, any of which may grow in local profusion, especially in well-drained, relatively open situations where their grassy competitors are not too abundant:

Puccinellia fasciculata (Torr.) Bick.	*Limonium carolinianum*
Triglochin maritima	*Plantago decipiens*
Atriplex patula hastata	*Solidago sempervirens*
Salicornia europaea	*Aster subulatus*
" *mucronata*	" *tenuifolius*
Suaeda maritima	

In addition to these, the salt meadow flora may include certain of the plants to be listed in connection with brackish meadows, these, however, being restricted in the main to the landward parts of the marsh. The character plants of salt meadows, like those of sea beaches, are distinctly xerophytic in their structure, and, except for the grass-like forms, all of them tend toward a succulent habit, the samphire (*Salicornia;* FIG. 8) being a leafless succulent of the most extreme type. Salt meadow plants apparently differ from beach plants,however, in being true halophytes: they are physiological rather than physical xerophytes.*

* Of special interest in the present connection is Kearney's paper ('18) on "Plant life on saline soils."

There is one peculiar feature of the upper littoral marsh which has already been suggested, and that is the occurrence, scattered here and there in greater or less abundance over the surface, of shallow depressions (FIGS. 7, 10), usually muddy or occupied by tidal pools at low tide, and strikingly different in the character of their vegetation from the adjoining higher and better drained parts of the meadow. These salt meadow pools and "rotten spots" (technically termed "pans"), the origin of which will be described

FIG. 7. Large pan in salt meadows becoming recolonized by local invasions of *Spartina glabra*. Westbrook.

later, may lack vegetation entirely, so far as the higher plants are concerned; and, while the alkali grass is frequently present, the salt meadow grass and the black grass are almost invariably absent. The character plants are usually two, namely the salt marsh grass and the samphire. Singly or in association, and not infrequently accompanied by the sea lavender (*Limonium*), these may predominate over considerable areas of undrained or poorly drained ground; but, even for them, the soil conditions are

not wholly favorable,* and very often they succumb to their manifestly unsuitable environment. The salt marsh grass, in such situations, commonly assumes a low, impoverished habit, often failing to flower, while the samphire and sea lavender grow much less vigorously than on better drained soils, frequently

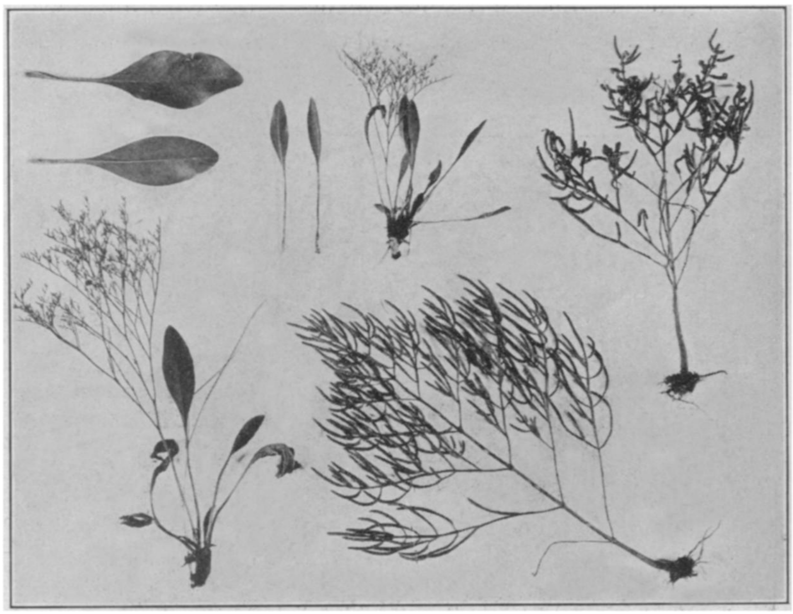

FIG. 8. *Salicornia europaea* (right) and *Limonium carolinianum* (left). The smaller specimens of each grew in a poorly drained depression, the larger ones in a well-drained situation, in a salt meadow. New Haven.

exhibiting a very sickly appearance (FIG. 8). In the absence of seed plants, salt meadow pools may support a dense population of algae—*Cladophora expansa* and various species of *Enteromorpha*, together with numerous smaller and less conspicuous forms. The bottom in shallow pools commonly is overgrown by felt-like masses of blue green algae, comprising such forms as *Lyngbya*, *Oscillatoria*, *Microcoleus*, and *Chroöcoccus*, and in muddy depres-

* While there seems little question that the paucity of seed plants in salt marsh depressions is associated with poor drainage, it has not yet been established just what factors (aëration, salinity, etc.) are directly responsible for the failure of various halophytic species to grow here. See, in this connection, Yapp and Johns ('17, p. 97), Shreve, Chrysler, etc. ('10, p. 131).

sions the surface of the ground often is similarly covered by a thin, tough mat of intricately interwoven algae.* Various minute algae, or larger species that have been washed in, may be present elsewhere on the surface of the meadow, but they are of relatively subordinate importance in their effect on the general aspect of the vegetation.

The supralittoral region.—Locally, and particularly where it borders on the mainland, the surface of a salt marsh may rise above the level reached by mean high tides. Where not influenced by seeping subterranean fresh water, these higher, drier supralittoral portions of the salt marsh may maintain an almost pure growth of the black grass; or, particularly in the fresher situations, they may be populated by such species as the following:

Panicum virgatum	*Aster novi-belgii littoralis*
Hierochloë odorata	*Baccharis halimifolia*
Spartina Michauxiana	*Iva oraria*
Teucrium canadense littorale	*Helianthus giganteus*
Solidago sempervirens	*Cirsium horridulum* Michx.

The vegetation of the mainland, where it abuts on the marsh, may also be made up very largely of the species just listed, or the ordinary upland vegetation may fringe directly on the marsh. Even in the latter case, however, there are a number of species which are particularly characteristic of salt marsh borders. Among the trees the post oak (*Quercus stellata*) and the sour gum (*Nyssa sylvatica*) are deserving of special mention: the former reaches in southern New England its northern limit of range and, except locally, never extends inland; the latter, also near its northern limit here, is especially conspicuous along the edges of the salt marshes, where it stands out in early autumn by reason of the gorgeous red color of its foliage. Other woody plants which should be listed here are as follows:†

Juniperus virginiana	*Quercus bicolor*
Smilax rotundifolia	*Celtis occidentalis*
Myrica carolinensis	*Sassafras variifolium*

* For further details regarding these algal felts and mats see B. M. Davis ('13), Johnson and York ('15), and Harshberger and Burns ('16).

† Favorable light relations probably are as important a factor as any in their influence on the character of the upland vegetation bordering salt marshes. Essentially all the species here listed are relatively intolerant of shade.

Pyrus melanocarpa	*Rhus typhina*
Amelanchier sp.	" *Toxicodendron*
Rosa humilis	*Clethra alnifolia*
Rhus copallina	*Gaylussacia baccata*

It very often happens that the ground along the edge of a salt marsh (supralittoral or upper littoral) is so saturated by underground fresh water that a swampy condition would prevail here, irrespective of the influence of tidal waters. In such cases the salt marsh proper is separated from the supralittoral fresh swamp by a region in which brackish marsh plants predominate. Many of these latter may extend well up into the supralittoral region, mingling here with the vegetation of the fresh water swamp (see later discussion of brackish swamps, etc.).

Muddy beaches.—Very often, in somewhat protected situations, the surface of an otherwise sandy or stony shore, in the littoral region, is somewhat muddy. Areas of this description (FIG. 2) can perhaps be regarded as incipient marshes, the actual development of typical marshland being prevented by currents or other local factors. The lower littoral along such a beach is frequently overgrown with salt marsh grass, although in other cases it is nearly barren, while the upper littoral usually supports various of the species characteristic of salt marshes, especially *Spartina patens*, *Salicornia europaea*, *Suaeda*, *Limonium*, and *Plantago*.

2. Associations of the brackish marsh series

The muddy bottoms and tidal flats of the sublittoral and lower littoral.—The eel grass commonly ranges well up into tidal creeks, but the characteristic plant of muddy bottoms in brackish waters is the ditch grass (*Ruppia maritima*), a form resembling the eel grass in general habit but much more delicate. This species also occurs here and there along the open Sound, in waters which are strongly saline (see Graves '08, pp. 122 et seq.), and, at the other extreme, it grows in waters that are only slightly saline. Even at its best, however, the *Ruppia* seldom approaches the more robust *Zostera* in mass effect. Another seed plant of shallow, brackish waters, sometimes growing in profusion and superseding *Ruppia* in the fresher waters, is the brackish water pondweed (*Potamogeton pectinatus*). In addition to these, *Vallisneria*

spiralis, *Zanichellia palustris*, *Potamogeton* spp., and various other aquatic seed plants of primarily fresh water habitats may extend seaward into waters that are perceptibly brackish. The algal flora of muddy bottoms and tidal flats in brackish waters lacks various of the species which elsewhere grow as epiphytes on *Zostera*, but the sea lettuce (*Ulva*) can grow in water which is quite fresh, and this plant, together with certain species of *Enteromorpha*, may make quite as prominent a display here as in the more saline situations.

The midlittoral marsh.—*Spartina glabra*, the character plant of the midlittoral region in salt marshes, exhibits a remarkably wide range of adaptability in relation to the salinity of the water which bathes its roots and shoots. Not only does it thrive in the most saline situations (generally speaking) but it is also capable of growing in habitats where the soil water is nearly fresh. Along the lower courses of fresh water streams it commonly reaches inland quite as far as the saline influence of the tidal waters, and in the majority of situations where the upper littoral region is occupied by brackish meadows the salt marsh grass maintains the commanding position in the midlittoral.* In waters which are but slightly saline the salt marsh grass comes into competition with such species as the bulrush (*Scirpus americanus*) and wild rice (*Zizania palustris*), but it is only where the brackish meadows and reed marshes of the upper littoral give way, upstream or inland, to fresh marshes that this grass becomes wholly replaced by other species. But one other plant need be mentioned here, viz., the water hemp (*Acnida cannabina*), a tall, stout, annual herb which is frequently associated with the *Spartina* in brackish waters, growing also at higher levels but principally along tidal streams.

Swamps of the upper littoral and the supralittoral regions.—The vegetation of the upper littoral region presents two fairly well defined aspects, namely, *meadow* and *reed marsh*. Brackish meadows are typically developed in the relatively more saline situations and differ little in general appearance from the true salt meadows of which they commonly are but continuations. Brackish reed marshes are best developed in the relatively fresher situations and

* It is a very common condition along tidal creeks, however, that the steep muddy banks of the midlittoral are practically destitute of seed plants.

are scarcely to be distinguished in general appearance from the fresh marshes into which they often merge. Between the brackish swamps of the upper littoral and those of the supralittoral it is impossible to draw any sharp line, and for this reason they have been grouped together. The supralittoral swamps (i.e., those beyond the reach of ordinary high tides) are distinguished chiefly by the greater abundance of plants which are associated primarily with fresh soil and by the practical absence of true salt marsh species. Most of the plants found here may be said to grow in fresh-to-brackish situations,† whereas most of the species of the upper littoral region may similarly be said to grow in salt-to-brackish situations (but some species of the upper littoral, such as *Solidago sempervirens*, are able to thrive in fresh as well as in saline soils). The appended remarks apply chiefly to the upper littoral.

Brackish meadows will be considered first. Locally and over considerable areas the salt meadow grass, alkali grass, and black grass, together with most of their associates in more saline situations, may be quite as prominent here as in salt meadows. Certain of the salt meadow species, particularly *Triglochin* and *Solidago*, are even commoner in brackish meadows, while but three of those listed on page 530, namely the two species of *Salicornia* and the *Limonium*, are perceptibly less frequent here. There is a marked tendency, however, for the salt meadow grasses to give way in brackish meadows to other grasses or grass-like forms, notably *Agrostis alba maritima*, *Eleocharis palustris*, and *E. rostellata*; and, especially in the fresher or higher parts of the meadows, these latter may predominate. Other seed plants which are more or less peculiar to brackish meadows, being found less frequently or not at all in typical salt meadows, are the following:

Cyperus Nuttallii	*Potentilla pacifica* Howell
Scirpus nanus	*Sabatia stellaris*
Polygonum exsertum	*Gerardia maritima*
" *aviculare littorale*	*Pluchea camphorata*
Spergularia marina	*Iva oraria*

Various of the bulrushes (*Scirpus americanus*, *S. Olneyi*, *S. campestris paludosus*, *S. robustus*) are locally abundant in brackish

† Plants which are capable of growing in either fresh or saline situations are designated "facultative halophytes" by Bartlett ('09).

meadows, growing in wet depressions and especially along the landward border of the meadow, in places where the ground is naturally very wet and swampy by reason of seeping underground water. In situations of the latter sort the vegetation bordering the meadow may be essentially that of brackish reed marsh (see below). Elsewhere, particularly where the substratum (upper littoral or supralittoral) is less wet and the ground water scarcely brackish much of the time, the meadow may be bordered by a fringe of predominantly lower vegetation, which includes, among others, various of the species listed below;* but there are all sorts of intergrading conditions:

Panicum virgatum	*Cicuta maculata*
Hierochloë odorata	*Ptilimnium capillaceum*
Cladium mariscoides	*Samolus floribundus*
Carex hormathodes	*Teucrium canadense littorale*
Lilium superbum	*Aster novi-belgii littoralis*
Iris prismatica	*Baccharis halimifolia*
Sanguisorba canadensis	*Iva oraria*
Oenothera linearis	

Poorly drained depressions in brackish meadows may support a flora similar to those in salt meadows; or they may be occupied by *Triglochin*, *Plantago*, *Spergularia*, and various species of *Scirpus*. The physical nature of the substratum in brackish meadows, as a rule, is essentially like that of salt meadows—a compact peat rendered more or less gritty by inorganic sediment.

Brackish reed marshes frequently form fringing borders along the landward edges of brackish meadows, but they cover extensive areas only along the lower courses of large streams. In places of this description there commonly are broad tracts of land, away from the river, from which the water, by which the ground is overflowed at high tide, is prevented from draining away rapidly by a slightly higher ridge of ground (for convenience, here termed the *marginal embankment*) that borders the river itself on either side (see Nichols, '15, p. 171). These tracts are usually occupied by a dense growth of cat-tails (especially *Typha*

* It is of interest to note that while certain of the species here listed (e.g., *Iris prismatica*, *Baccharis halimifolia*, *Iva oraria*) are restricted to the vicinity of the seacoast, and while most of them are best developed here, the majority of them also are found in interior portions of this continent, particularly in the Mississippi basin and in the Great Lakes region.

angustifolia) or of the reed (*Phragmites communis*), together, particularly in the drier situations (as, for example, on marginal embankments) with the slough grass (*Spartina Michauxiana*). The rose mallow (*Hibiscus Moscheutos*) often occupies a prominent position here, as also along the landward edges of brackish meadows, and the wild rice may predominate in the fresher situations.

The swamps of the *supralittoral region* may be essentially similar in their vegetation to the brackish meadows and marshes which have just been described; but swampy situations in the supralittoral, even where exposed to periodic inundation by somewhat brackish water, are often wooded. As already suggested, the explanation of this fact, as well as of the occurrence, on drier but occasionally overflowed uplands adjoining both salt and brackish meadows, of various trees, shrubs, and herbaceous plants which are distinctly non-halophytic, seems to be this: that "while the surface marsh soil may be strongly saline, the subsoil is controlled by fresh water which flows outward from the higher ground under the salt marsh sod" (Harshberger, '11, p. 487). In the case of many plants which thus appear to be flourishing in an essentially halophytic environment, it may therefore be only the shoots—organs which are incapable of absorption and hence but little affected—that are actually exposed to the unfavorable influence of the saline water.

Muddy tidal shores.—In addition to the plants described in preceding paragraphs, there are a number of forms which are generally described as growing along muddy tidal shores rather than in the marshes. These plants are especially characteristic of brackish tidal shores along rivers, and for the most part are rather local in their occurrence. The following are representative:

Lophotocarpus spongiosus	*Tillaea aquatica*
Heteranthera dubia	*Lilaeopsis lineata*
Ranunculus Cymbalaria	*Limosella aquatica*

3. Associations of the fresh marsh series

Introductory.—Fresh water coastal swamps may be either marshy or wooded. Wooded coastal swamps scarcely differ from wooded swamps inland and merit no special comment here, but the fresh water marshes of the coast present certain distinctive

features. Particularly is this true of marshes which are of estuarine origin, and these will be taken as representative of the fresh water series. *Fresh water estuarine marshes* occur along parts of fresh water streams which are subject to tidal fluctuations but are beyond the influence of saline waters. They may occupy low grounds of any description, but are most typically developed in situations which are topographically similar to those elsewhere occupied by brackish reed marshes. Along the Connecticut and Quinnipiac rivers they make their appearance a few miles above the river's mouth, further upstream passing into flood plain swamps.*

The sublittoral region.—The vegetation of the river bottom below low tide level comprises various aquatic seed plants, especially the wild celery (*Vallisneria spiralis*) and divers pondweeds (*Potamogeton* spp.). Locally, in quiet waters, the water lilies (*Nymphaea advena* and *Castalia odorata*) may be abundant. Other common aquatics, such as the water weed (*Elodea* sp.) and *Najas flexilis*, are variously represented. The bottom vegetation is well developed only in shallow, slow-flowing waters.

The lower littoral and midlittoral marsh.—The character plant here is the wild rice (FIG. 9). Along muddy stream borders and in sloughs, in water ranging from a few inches to more than two feet deep at high tide, this magnificent grass, sometimes nearly ten feet high, commonly forms a luxuriant growth. With it, especially in the shallower water, may grow various of the species listed below:

Sparganium spp.	*Peltandra virginica*
Sagittaria latifolia	*Orontium aquaticum*
" *graminea*	*Pontederia cordata*
Echinochloa Walteri	*Polygonum acre*
Leerzia oryzoides	*Sium cicutaefolium*
Scirpus americanus	*Bidens laevis*

* Here, as elsewhere, the transition from one type of swamp to another is gradual, and there are all intermediate degrees between the typical salt marshes which prevail near the mouth of the river and the typical flood plain swamps which characterize portions of the river above tide water. As in the salt marshes, the substratum in an estuarine marsh, whether brackish or fresh, usually is more or less peaty, but any attempted line of demarcation between fresh estuarine swamps and flood plain swamps, where the substratum is practically pure alluvium, must be quite arbitrary.

On the whole these latter plants are of relatively subordinate ecological importance, but certain of them, e.g., *Orontium*, frequently predominate locally.

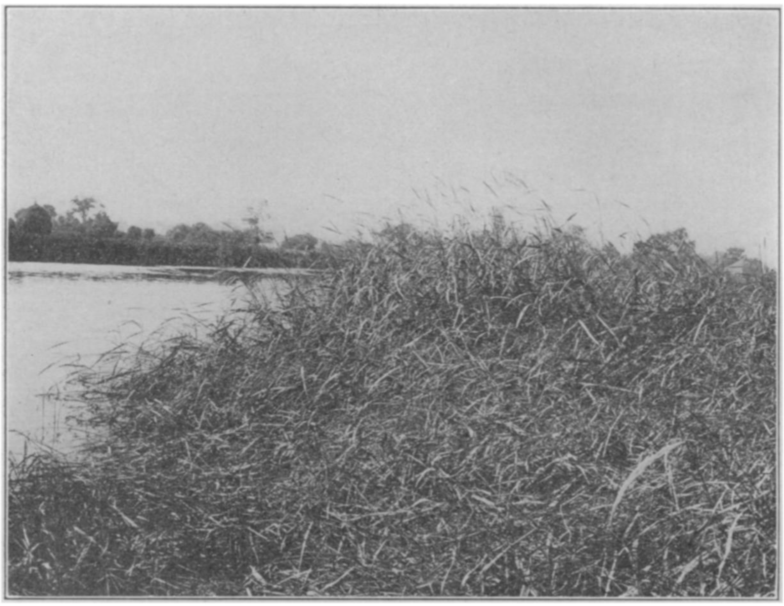

FIG. 9. *Zizania palustris* fringing an estuarine marsh along the Quinnipiac River. North Haven.

The upper littoral marshes and meadows.—In typical cases the vegetation of the upper littoral region, which includes the greater part of the swamp surface, is predominately reed-like in the vicinity of the river and in the lower situations, tending to assume a meadow-like aspect away from the river and in the higher situations. Of the reed-like forms, the cat-tails (*Typha latifolia* and *T. angustifolia*) are the commonest representatives, and the cat-tail associations, together with the wild rice associations of the wetter situations, comprise the most distinctive association-types of *estuarine fresh marshes*.* The following plants, among others, are commonly associated with the cat-tails in fresh coastal marshes, either as scattered individuals or as local dominants:

* Harshberger ('19) likens marshes such as these to the British "fens," and proposes that they be so designated.

Aspidium Thelypteris	*Rumex Brittanica*
Phragmites communis	*Impatiens biflora*
Scirpus validus	*Hibiscus Moscheutos*
" *cyperinus*	*Cicuta maculata*
Iris versicolor	*Lysimachia terrestris*
Juncus brevicaudatus	*Lycopus* spp.

The vascular plants in the subjoined list may be taken as representative of the flora of *estuarine fresh meadows*, as well as of coastal fresh meadows elsewhere. The list is far from complete.

Onoclea sensibilis	*Polygonum sagittatum*
Osmunda cinnamomea	*Verbena hastata*
Calamagrostis candensis	*Galium Claytoni*
Carex stricta	*Eupatorium purpureum*
Juncus effusus	" *perfoliatum*
Lilium superbum	*Aster novi-belgii*
Polygonum arifolium	" *puniceus*

Any of these meadow species may also grow in association with the cat-tails, as may certain of the forms listed for the mid-littoral region. Fresh water cat-tail marshes, like the meadows, are by no means restricted to estuarine situations, but are variously distributed along the coast.

The supralittoral region.—There is only one portion of the supralittoral that merits special comment, and this is the marginal embankment. Although the height of the surface here is but slightly greater, as a rule, than that of the upper littoral marsh, which it tends to cut off from the midlittoral marsh along the river, the difference in elevation and drainage may be quite sufficient to have a marked effect on the vegetation. Not only are sundry herbaceous plants found more frequently here than elsewhere, but the marginal embankment often stands out conspicuously by reason of its woody vegetation. Shrubs and trees may occur scattered locally through parts of the marsh away from the river, but along the channel they commonly form a prominent fringe of vegetation. The trees here include the willows (*Salix nigra*, *S. alba vitellina*), the elm (*Ulmus americana*), and various other species elsewhere characteristic of flood plains or river swamps. A list of representative herbaceous and shrubby species is given below.

HERBACEOUS SPECIES

Phalaris arundinacea	*Vernonia noveboracensis*
Spartina Michauxiana	*Mikania scandens*
Elymus spp.	*Aster paniculatus*
Lobelia cardinalis	*Ambrosia trifida*

SHRUBS

Salix lucida	*Cornus Amomum*
" *longifolia*	*Clethra alnifolia*
Alnus rugosa	*Cephalanthus occidentalis*
Rosa carolina	*Sambucus canadensis*
Ilex verticillata	*Viburnum dentatum*

4. Successional relations along depositing muddy shores

Introductory.—In discussing this phase of the subject attention may be confined to the salt marshes, brackish and fresh marshes being neglected. Generally speaking, a salt marsh seems to originate through the accumulation of silt and organic debris at lower levels and the consequent elevation of the substratum to a height at which the salt marsh grass is able to establish itself. Except for the prominent part played here by the accumulation of silt, the manner in which muddy bottoms along the seacoast become built up is essentially similar to that in which many lakes become filled in during their conversion into swamps (see Nichols, '15). There is a close analogy to the early stages in the development of a flood plain (see Nichols, '16), except that, in the present case, vegetation plays a more active part and the inorganic debris is much finer. Plants assist in the building-up process in two ways: first, through their mechanical interference with tidal currents, retarding these and causing them to deposit their load of silt; second, through the accumulation of their own dead remains.

The apparent succession of plant associations.—Assuming our salt marshes to have originated in the manner just suggested, it would very naturally be inferred that as the substratum has been gradually built up to successively higher elevations and as the environmental conditions of the habitat have thereby undergone progressive alteration, the rising ground has been successively occupied, in order, by the associations (or groups of associations) elsewhere described as characteristic of the sublittoral, the lower littoral, the midlittoral, and the upper littoral regions. In other words, it would seem that the historic succession of plant associa-

tions during the development of the marsh must have followed the same order as the zoned series of associations which is to be encountered along the outer edge of most marshes, in proceeding from the muddy bottoms of the sublittoral upward to the grassy meadows of the upper littoral. As will be brought out presently, however, this hypothetical correspondence, though formerly accepted as a fact (see Shaler, '85, etc.), would seem to be merely apparent.

The actual succession of plant associations and its probable explanation.—In attempting to work out the successional relations of any given series of plant associations there are various methods of procedure, but all of those customarily employed necessarily are based on the study of the existent vegetation. In the large majority of cases, therefore, conclusions regarding the nature of any given successional series, where this extends over a period of time beyond that during which the area in question is actually under observation, must be founded wholly on circumstantial evidence. It is of course inevitable that any deductions regarding the future course of succession should be largely hypothetical, and, except in the comparatively few instances where historic records are available or where a fossil record has been left by successive generations of preëxistent plants, any reconstruction of the course of events in the past must likewise be largely assumed from theoretical deductions. Salt marshes, however, resemble peat bogs in that conditions have favored the preservation of a fossil record, since they are usually underlain by peat deposits which may extend to a depth of many feet, and the study of these salt marsh peat deposits has yielded some very significant facts.

Assuming the vertical or historic order of succession during the development of the marsh to have been coördinate with the present day lateral sequence of zones, as set forth in the second paragraph above, the peaty and mucky deposits underlying a salt marsh should show approximately the following sequence of layers, from below upward: (1) a layer of silt, with remains of eel grass, extending from a variable depth to low tide level; (2) a layer of silt, with but few vegetable remains, extending from low tide level up to the level at which the salt marsh grass becomes established; (3) a layer of muddy peat with more or less abundant

remains of salt marsh grass, extending upward nearly to mean high tide level; (4) a layer of peat made up largely of the remains of the salt meadow grasses. But the actual examination of sections of salt marsh peat along the New England coast has revealed a very different state of affairs. Bartlett ('09), for example, describes a salt marsh near Woods Hole in which the salt marsh peat near the surface is underlain by the remains of a former *Chamaecyparis* bog, the stumps of large numbers of trees being preserved *in situ*. C. A. Davis ('10) reports that in the vicinity of Boston the peat deposits underlying the salt marshes likewise consist, in many cases, of the remains of fresh water vegetation; in other cases peat deposits composed largely of the remains of salt meadow grasses extend from the surface downward to a depth below that of mean low tide level—in other words, to a depth many feet lower than that at which the plants which formed the peat could possibly have grown. In no case, Davis emphatically states, does the peat show the hypothetical arrangement of layers specified above. The peat underlying a brackish meadow near New Haven, and sectioned during operations for brick clay, shows similar conditions: just beneath the surface (1) a thick layer of *Spartina patens-Juncus Gerardi* peat, followed in order below by (2) a layer of *Distichlis* peat and (3) a layer made up largely of cat-tai and fern remains, with (4) numerous scattered stumps resting in place on the underlying gravelly substratum, about five feet below the present mean high tide level.

From the foregoing observations it is clear that any assumed agreement between the present-day zonation of salt marsh associations in relation to tide levels and the succession of plant associations which has ensued during the development of the marshes, along the New England coast, is not in harmony with the facts as recorded by the underlying peat deposits, in so far as these records have been made available. By most authors, including Ganong ('03), Penhallow ('07), Bartlett ('09, '11), C. A. Davis ('10), Townsend ('13), and Johnson and York ('15), this discrepancy is explained as being due to coastal subsidence, abundant evidence (botanical and otherwise) tending to indicate that the land along the Atlantic coast has been gradually sinking at the rate of a foot or more per century. It is quite obvious that subsidence at a

rate more rapid than that at which the marsh surface is being built up would lead to an order of succession more or less completely the reverse of the apparent order earlier outlined, i.e., the succession of plant associations would be retrogressive; and, further, that a rate of subsidence exactly counter-balancing that at which the marsh surface is being built up would favor a complete absence of change in the character of the surface vegetation, i.e., there would tend to be no succession whatever. Only where the rate of upbuilding exceeds that of submergence could the actual succession of plant associations be expected to coincide with the apparent succession, i.e., only under these conditions could a progressive succession take place; and whether any such correlation ever actually exists remains to be demonstrated. The coastal subsidence explanation for the invasion of fresh swamps by salt water, and similar phenomena, is scouted by D. W. Johnson ('13), who would account for the observed facts in other ways; but Johnson's arguments are not wholly convincing.

Origin of salt marsh depressions, or "pans."—Mention has been made in an earlier paragraph (p. 531) of the occurrence, particularly in the meadows of the upper littoral, of poorly drained depressions, which differ greatly in the character of their vegetation from adjoining portions of the marsh (FIGS. 7, 10). The origin of these depressions, which range in depth from a fraction of an inch to well over a foot, has been variously accounted for. Harshberger ('16) attributes them to masses of tidal trash (consisting commonly of dead stems and leaves of eel grass and salt marsh grass, but in many cases—see Johnson and York, '15—made up largely of loose-floating *Ulva* and *Enteromorpha*) which in times of exceptionally high water are swept in over the surface of the meadow by tidal currents and, settling down there (particularly in places where the vegetation already has become matted and twisted by winds and waves, as shown in FIG. 6), smother out the existing plant cover. Subsequently, he maintains, rapid decay sets in, affecting not only the aerial plant organs but the underground parts as well, and eventually a depression of some depth may thus arise. This explanation, which is also suggested by Johnson and York ('15, pp. 21, 22, 47, etc.), accounts in a wholly satisfactory manner for the origin of the essentially flat barren spots, which are of frequent

occurrence in salt meadows, and a similar explanation accounts, in large measure, for the presence in the midlittoral marsh, in areas otherwise densely populated by salt marsh grass, of open patches (see FIG. 5), bare and muddy at low tide and frequently of considerable dimensions. It may perhaps account also for the origin of some of the shallower depressions in the meadows of the upper littoral; but many, if not most, of these latter, and the majority, if not all, of the deeper depressions, have arisen in a very

FIG. 10. Development of pans through local invasion of tidal creeks and ditches by *Spartina glabra*. Westbrook. In view to right a former meandering creek has become quite obliterated. Ditch in center has become completely obstructed; the one to left is still open.

different manner. Recent detailed studies by Yapp and Johns ('17) on the origin of these "pans" (as the depressions are termed by them and by other European ecologists) in the salt marshes of the Dovey Estuary, in Wales, have fully confirmed conclusions which the writer had already reached regarding their origin in the salt marshes along the Connecticut coast.

Avoiding detail, as far as possible, the pans of the upper littoral meadows may be divided into two groups, with reference to their mode of origin: primary pans, which are formed during the development of the marsh; and secondary pans, which arise subsequently. *Primary pans* are formed in somewhat the following manner. During the early development of the marsh, the

salt marsh grass, instead of forming a zone of vegetation directly continuous with that at higher levels along the shore, frequently grows in a more or less continuous belt at some little distance offshore, being separated from the higher portions of the shore by an area, of variable width but sometimes as much as a dozen yards across, or even more, in which the ground is practically destitute of seed plants (this condition is suggested in FIG. 2).* As the portion of the shore occupied by the grass becomes built upward, this plantless portion lags behind, eventually giving rise to a water-filled depression in the mature marsh. In one of the Cape Breton salt marshes studied by the writer (see Nichols, '17, FIG. 45; also Harvey, '19, FIG. 3) these depressions have persisted in the mature marsh as elongated lagoons of open water. But more commonly they become broken up and in part obliterated, during the growth of the marsh, through local invasions of the salt reed grass: indeed, small areas commonly become hemmed in by the salt reed grass at a very early stage in the development of the pan. *Secondary pans* may arise in several ways, one of which has already been described. In many cases (FIG. 7) their formation results from the relatively rapid building up of the ground along the margins of tidal streams, with the consequent ponding back of the water, between tides, in the lower parts of the meadow, away from the stream (see, in this connection, Nichols, '15, pp. 171, 172; also p. 537 of the present paper). Very commonly, also, they arise through the local invasion and obstruction of shallow tidal creeks by the salt marsh grass, a method of development graphically brought out by FIG. 10. Occasionally they seem to originate as ox-bows, in the usual manner, from meandering tidal creeks.

The fate of these pans need not be traced in detail. Unchanging though it may appear, the surface of a salt marsh, from year to year, is in a constant state of alteration. Erosion here and deposition or peat accumulation there tend to bring about changes in drainage and elevation which in turn react on the vegetation. In the shifting course of events the pans of today are destined, sooner or later, to vanish, while other areas, now occupied

* The absence of plants here is commonly due to the periodic accumulation along the shore of wave-washed drift, after the manner already described (pp. 545, 546).

by typical salt meadow vegetation, may become transformed into pans. And, in conclusion, it is needless to more than remark that, as a result of artificial ditching operations, which have become more and more prevalent in recent years, the pans, a natural breeding place for mosquitoes, are destined to undergo even more rapid changes than those above suggested.

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